

Fossil red deer *Cervus elaphus* from the sea-floor of the East China Sea off Amakusa-shimoshima Island, southwestern Kyushu, Japan

RYU KUWAYAMA¹, TOMOWO OZAWA¹ and HIROYUKI OTSUKA²

¹Department of Earth and Planetary Sciences, Graduate School of Science, Nagoya University, Furo-cho, Chikusa-ku, Nagoya 464-8602, Japan

²Department of Earth and Environmental Sciences, Faculty of Science, Kagoshima University, Korimoto 1-21-35, Kagoshima 890-0065, Japan

Received 1 September 1996; Revised manuscript accepted 9 February 1998

Abstract. A skull of a fossil deer dredged from the sea-floor of the East China Sea off Ushibuka City, Kumamoto Prefecture, southwestern Kyushu, Japan is identified by the size and shape of its pedicles as the red deer *Cervus elaphus*, presently living on the Eurasian and North American continents. This is the first well-documented fossil record of red deer from Japan, although less reliable and doubtful fossil occurrences of the species have previously been reported from the Pleistocene of central Japan. A ¹⁴C date of 19,780 ± 190 yr BP was obtained for collagen fractions extracted from the fossil skull of *C. elaphus* using a Tandetron accelerator mass spectrometer. The geologic age of the fossil agrees with the accepted ¹⁴C age of the Last Glacial maximum. The present finding of the fossil red deer strongly indicates that during the Last Glacial maximum the Asian continent and Kyushu were connected by a land bridge in the northern part of East China Sea.

Key words: *Cervus elaphus*, glacial period, Japan, land bridge, late Pleistocene, skull

Introduction

In 1990, a well-preserved partial skull of a fossil deer was dredged by a fisherman from a depth of about 160 m in the East China Sea off Ushibuka City, Kumamoto Prefecture, southwestern Kyushu, Japan (Figure 1). Several other fossil remains including an elephant tusk have been recovered from the sea-bottom of this area, and a number of fossil mammals such as *Palaeoloxodon naumanni* and *Elaphurus mayai* have also been dredged from other area in the East China Sea (Otsuka, 1982; Otsuka, 1987). The fossil deer was loaned to us for study through the courtesy of Tetsuro Tateshi in Ushibuka City. Our comparative morphological study has confirmed that the fossil specimen is referable to the red deer *Cervus elaphus* Linnaeus, presently living in Eurasia and North America (Figure 2). In East Asia, occurrences of fossil red deer are very rare, being known from the middle Pleistocene of Tingtsun in China and Tologoy in Russia (Pei *et al.*, 1958; Vangengeim and Sher, 1971) and from the upper Pleistocene of Sjara-osso-gol, Choukoutien (Upper Cave) and Ku-hsiang-tung in China (Boule *et al.*, 1928; Pei, 1940; Tokunaga and Naora, 1939). In Japan, poorly-preserved fragments of a mandible and an antler referred to the red deer have been reported from the Upper

Kobiwako Group of middle Pleistocene age (Shikama, 1941) and the upper Kuzuū Formation (Shikama, 1949) of late Pleistocene age, respectively. However, these fossils are too incomplete to unequivocally identify them as *Cervus elaphus*. This paper confirms for the first time that red deer once lived in Japan and adds information about the dispersal area of *Cervus elaphus* in the Pleistocene of Eurasia.

Systematic description

Order Artiodactyla Owen, 1848
Family Cervidae Gray, 1821
Subfamily Cervinae Gray, 1821
Genus *Cervus* Linnaeus, 1758

Cervus elaphus Linnaeus, 1758

Figures 3, 4

Cervus canadensis Erxleben. Matsumoto, 1926, p. 35-37, pl. 12 (1), figs. 7-10; Boule *et al.*, 1928, p. 55-57, pl. 12, figs. 2-4, pl. 13, fig. 5; Pei, 1940, p. 68-71, text-figs. 34-36, pl. 8, figs. 3, 4; Pei *et al.*, 1958, p. 34-36, text-fig. 9, pl. 2, fig. 2.
Cervus elaphus Linnaeus. Tokunaga and Naora, 1934, p. 64, pl. 17, figs. 3, 5; Tokunaga and Naora, 1939, p. 45, 46, text-fig.

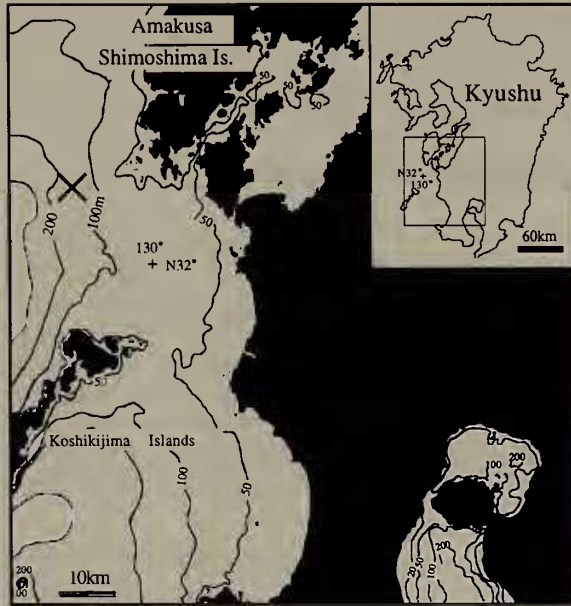


Figure 1. Map showing the collecting locality (X) of the fossil red deer skull in the East China Sea off Amakusa-Shimoshima Island, southwestern Kyushu, Japan.

12, pl. 1, fig. 16, pl. 3, fig. 9.

(Synonymy includes only citations of fossil remains recovered in East Asia.)

Material studied.—A fragment of an adult male skull including the neurocranium and part of the frontals with pedicles (Ushibuka City Kaisaikan Museum, UCKM-V-1) (Figure 3); collected from the sea-floor of the East China Sea off Ushibuka City, Kumamoto Prefecture, Japan. ^{14}C date: $19,780 \pm 190$ yr BP (Laboratory code number NUTA-

5266)

Description.—The neurocranium is large and wide, measuring 83.6 mm in width and 73.1 mm in height. In lateral view, the angle between the parietal and frontal is 113.5° . The minimum width of the frontals is 108.5 mm. The dorsal surface of the parietal joins the posterior surface of the occipital almost perpendicularly. The interfrontal suture is somewhat protruding and notched. The sagittal suture is partly fused and is recognized as a zigzag line between the parietal bones. The supraorbital foramina are ellipsoidal in shape and located at central part of the frontals. The maximum width between the supraorbital foramina is 67.0 mm. The sulci above them are not very deep and extend obliquely and slightly upward.

The pedicles are very stout especially at their bases. They are short and in lateral view do not protrude and overhang the parietal surface. The antero-posterior diameters of the pedicles (36.5 mm on the right and 37.9 mm on the left) are a little smaller than their transverse diameters (40.0 mm on the right and 41.0 mm on the left). The angle of pedicle diversion is 66° . The minimum distance between the pedicles measures 78.1 mm. In lateral view the pedicles are slightly inclined backwards. The surface of the pedicles is marked by a number of thin vertical sulci.

The roof of the neurocranium is well developed. In dorsal view it appears clearly depressed in front of the occipital and at the level of the temporal bone. In lateral view the occipital condyles are quite convex, although the surface of the occipital is slightly convex. In posterior view the occipital condyles have blunt outlines except for their lower ends, so that each of their lateral margin becomes gradually narrower ventrally. The medial margins of the occipital condyles are parallel with each other. The dorsal margin of the foramen magnum curves downward on either side of the midline. The dorsal margin of the occipital shield is gently convex.

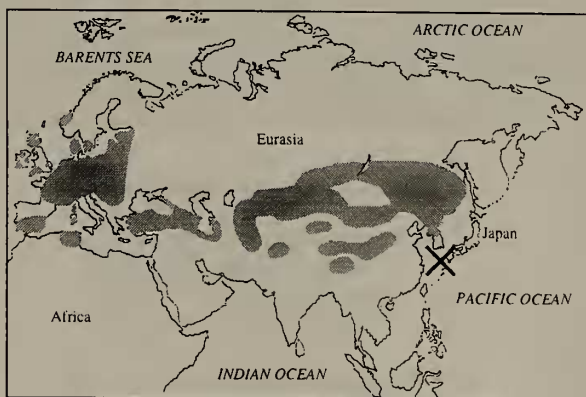
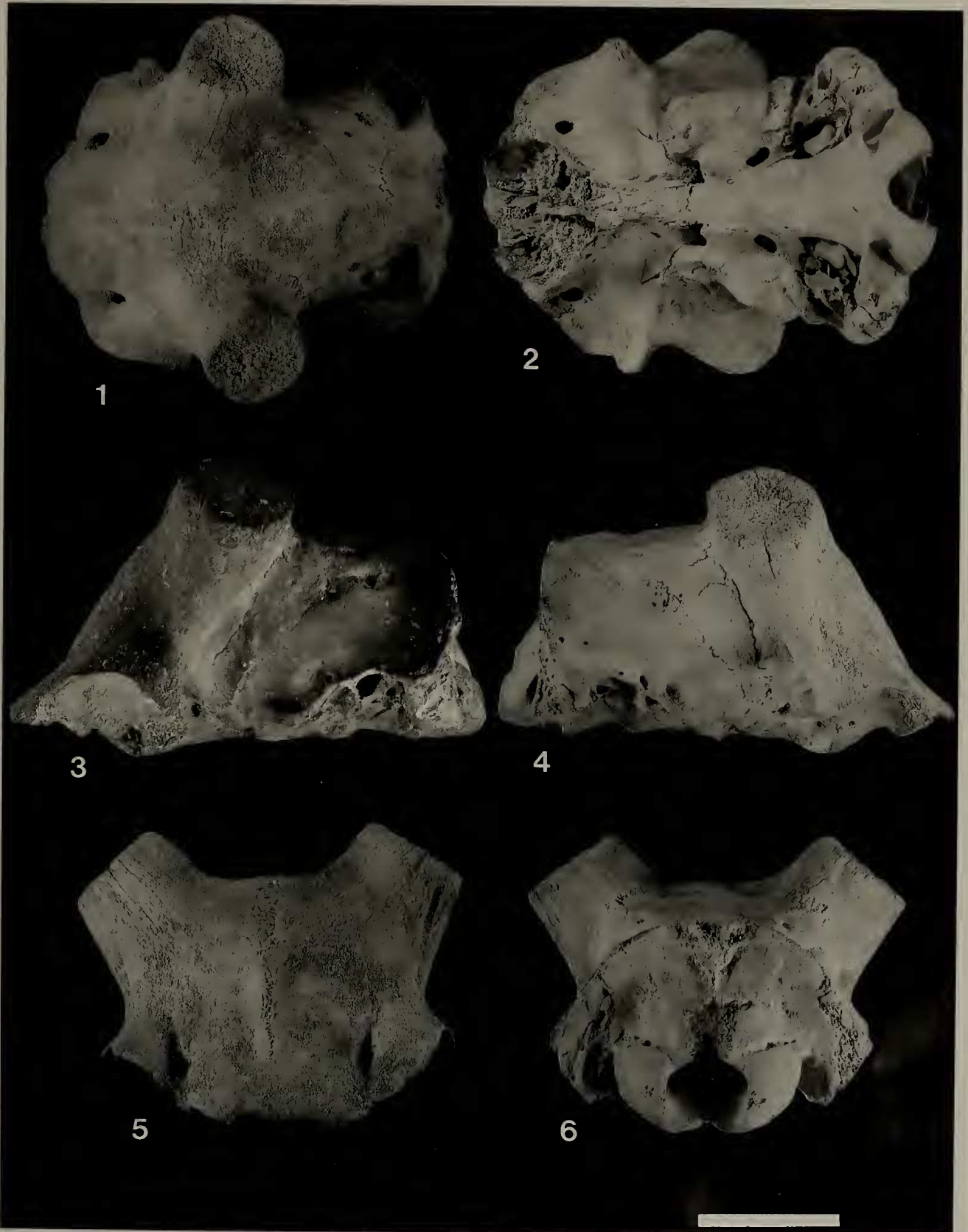
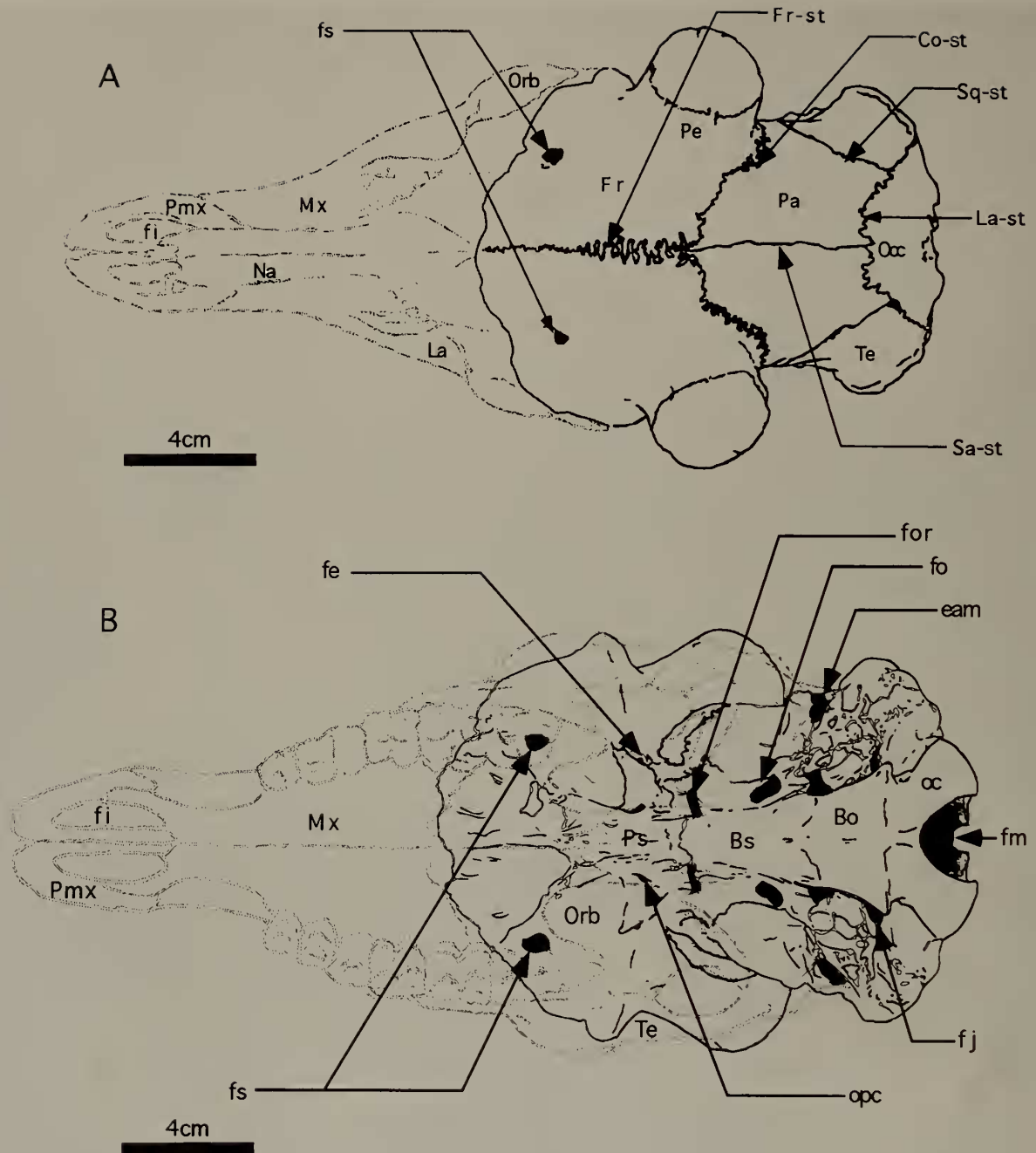


Figure 2. Map showing the distribution of the fossil and living red deer. Dotted area: the distribution of living red deer (after Whitehead, 1972). X: the locality of fossil red deer studied in this paper.

Figure 3. *Cervus elaphus* Linnaeus. Partial adult male skull consisting of the neurocranium and part of the frontals with pedicles (UCKM-V-1) from the sea-floor of the East China Sea off Ushibuka, Kyushu. 1: Dorsal view, 2: Ventral view, 3: Left lateral view, 4: Right lateral view, 5: Frontal view, 6: Posterior view. Scale bar equals 4 cm.





In ventral view the occipital condyles are bluntly rounded. The occipital condyles and the basioccipital are bounded by a well-developed constriction. The tubercles for the muscular insertions are well inflated. The oval foramina are elongate, ellipsoidal in shape and their anterior margins are inclined inwards.

Measurements.—Basic morphology and measurements adopted in this paper are presented in Figure 5 and Table 1.

Comparisons.—Comparisons have been made with the

living and fossil Cervidae including 14 species and 24 subspecies among 5 genera. To avoid the effect of sex and age difference, we only used male adult skulls except for a female individual of *Cervus (Axis) axis* Erxleben from India housed in the Nagoya Higashiyama Zoo, Japan. Some scientists considered that the European red deer is specifically distinguishable from the Asian and North American red deer on the basis of external morphology (Whitehead, 1972; Putman, 1988). Lowe and Gardiner (1989), however, consid-

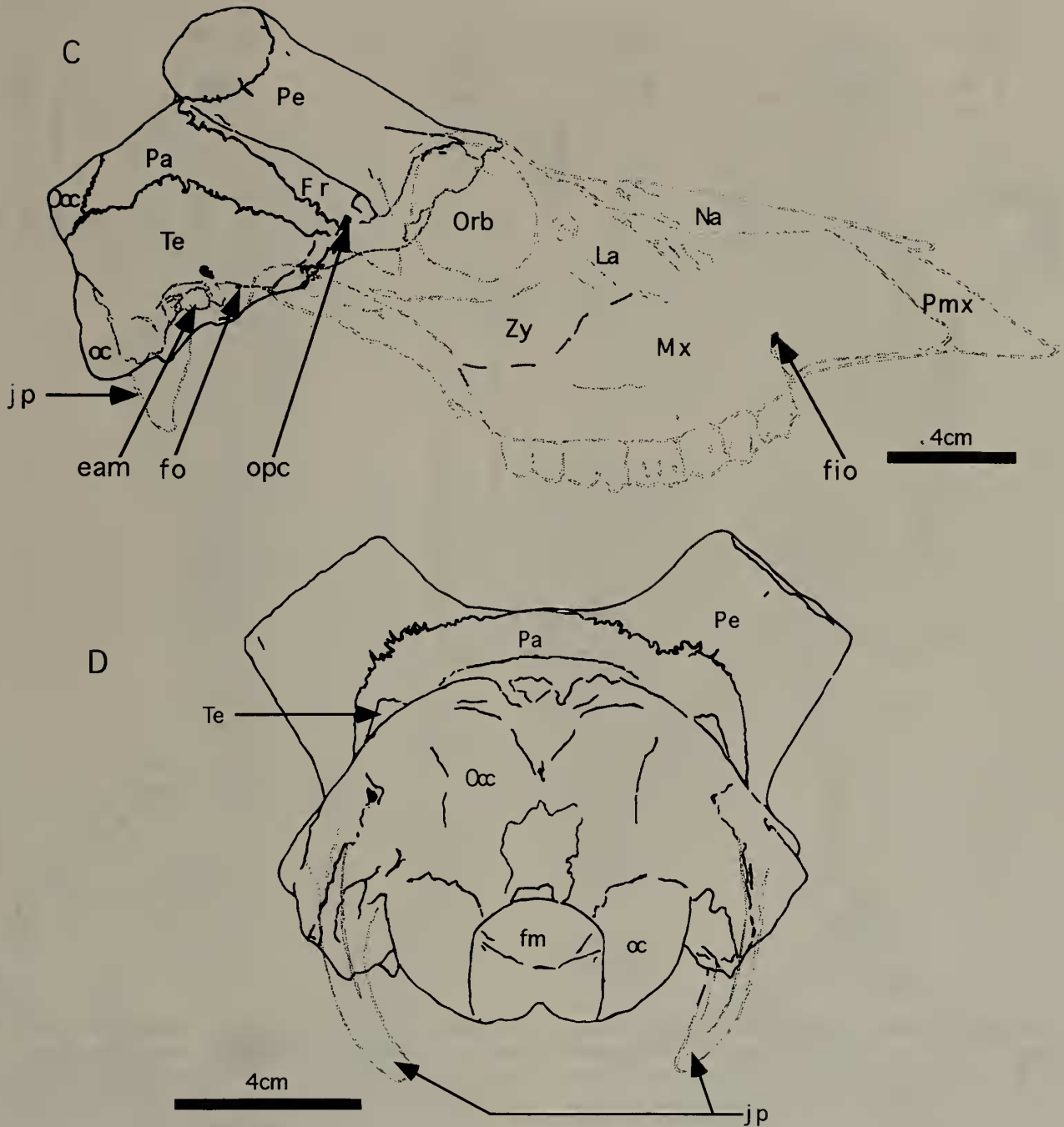


Figure 4. Restoration of the fossil skull of *Cervus elaphus*. **A:** dorsal view, **B:** ventral view, **C:** right lateral view, **D:** posterior view. Solid line: a part of skull preserved as the fossil specimen, Dotted line: broken parts. Bo=basioccipital, Bs=basisphenoid, Co-st=coronal suture, eam=external acoustic meatus, fe=ethmoidal foramen, fi=incisive foramen, fio=infraorbital foramen, fj=jugular foramen, fm=foramen magnum, fo=oval foramen, for=orbital round foramen, Fr=frontal, Fr-st=frontal suture, fs=supraorbital foramen, jp=jugular process, La=lacrimal, La-st=lambdoid suture, Mx=maxilla, Na=nasal, oc=occipital condyle, Occ=occipital, opc=optic canal, Orb=orbital, Pa=parietal, Pe=pedicle, Pmx=premaxilla, Ps=presphenoid, Sa-st=sagittal suture, Sq-st=squamosal suture, Te=temporal, Zy=zygomatic.

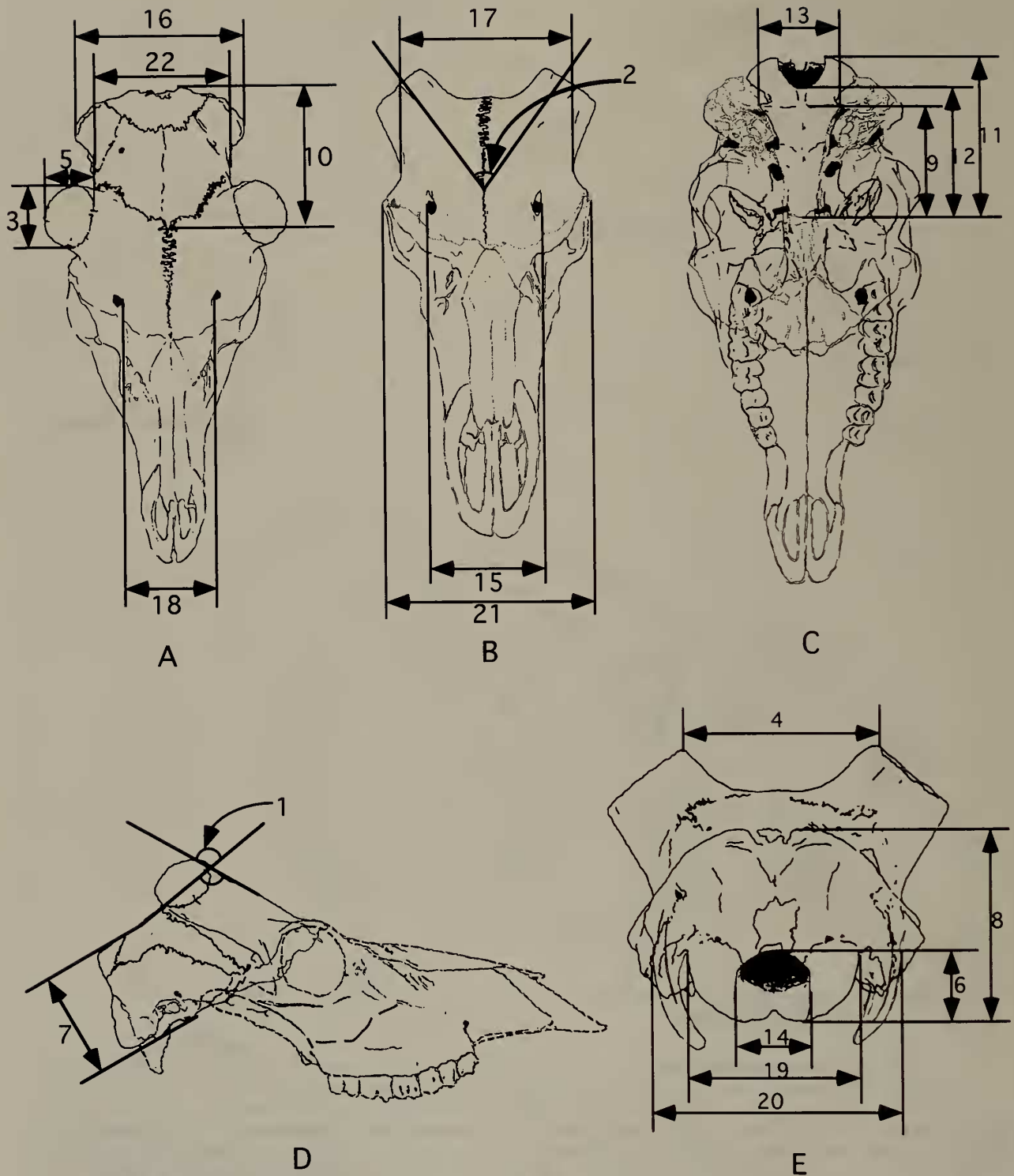


Figure 5. Location of measurements taken of the fossil skull of *Cervus elaphus*. A: dorsal view, B: frontal view, C: ventral view, D: right lateral view, E: posterior view. See Table 1 for explanation of the measured parts.

Table 1. Measurements of the skull of fossil red deer following Dreisch (1976). For measured parts see Figure 5. (1) ang fr-par: angle between frontal and parietal plane, (2) ang ped: angle of pedicle diversion, (3) dap ped: antero-posterior diameter of the pedicles, (4) dis ped: minimum distance between pedicles, (5) dt ped: transverse diameter of the pedicles, (6) h fm: height of the foramen magnum, (7) h neu: neurocranium height, (8) h occ: occipital height, (9) l bas: basioccipital length, (10) l i-br: inion-bregma length, (11) l max sph-occ: maximum length of sphenoid-occipital, (12) l min sph-occ: minimum length of sphenoid-occipital (=basicranial axis), (13) w bas occ: basioccipital width, (14) w fm: width of the foramen magnum, (15) w max fs: maximum width between supraorbital foramina, (16) w max neu: maximum neurocranium width, (17) w min fr: minimum frontal width, (18) w min fs: minimum width between supraorbital foramina, (19) w oc: external width of the occipital condyles, (20) w occ: occipital width, (21) w orb: skull width at the orbital level, (22) w par: neurocranium width (=parietals width).

Measured parts	in mm/degree	Proportion	Ratio
1) ang fr-par	113.5		
2) ang ped	66.0		
3) dap ped (right)	36.5	dap ped (r)/w occ	0.41
3) dap ped (left)	37.9	dap ped (l)/w occ	0.43
4) dis ped	78.1	dis ped/w occ	0.88
5) dt ped (right)	40.0	dt ped (r)/w occ	0.45
5) dt ped (left)	41.0	dt ped (l)/w occ	0.46
6) h fm	25.0	h fm/w occ	0.28
7) h neu	73.1	h neu/w occ	0.82
8) h occ	71.6	h occ/w occ	0.81
9) l bas	61.7	l bas/w occ	0.70
10) l i-br	85.9	l i-br/w occ	0.97
11) l max sph-occ	86.0	l max sph-occ/w occ	0.97
12) l min sph-occ	69.8	l min sph-occ/w occ	0.79
13) w bas occ	43.7	w bas occ/w occ	0.49
14) w fm	25.5	w fm/w occ	0.29
15) w max fs	67.0	w max fs/w occ	0.76
16) w max neu	108.2	w max neu/w occ	1.22
17) w min fr	108.5	w min fr/w occ	1.22
18) w min fs	58.0	w min fs/w occ	0.65
19) w oc	61.0	w oc/w occ	0.69
20) w occ	88.6		
21) w orb	125.2	w orb/w occ	1.41
22) w par	83.6	w par/w occ	0.94

ered that it is impossible to distinguish both groups clearly at the species level based on the skull morphology. In this study we have treated both groups of the red deer as the same species *Cervus (Cervus) elaphus* following the opinion of Lowe and Gardiner (1989).

The fossil skull UCKM-V-1 clearly preserves characters typical of the subfamily Cervinae, especially the genus *Cervus*. The shape of the basioccipital and occipital condyles closely resemble those of species of the genus *Cervus*. The ratios of external width of the occipital condyles/occipital width (0.69), occipital height/occipital width (0.81) and minimum length of sphenoid-occipital/occipital width (0.78) of the specimen fall within the known range of species of *Cervus* (0.65–0.77, 0.71–0.87, 0.70–0.84, respectively). The fossil skull is much larger than living and fossil sika deer from Japan and roe deer from Korea such as *Cervus (Sika) nippon nippon* Temminck from Kirishima of mainland Kyushu, C. (S.)

n. centralis Kishida from Chichibu, C. (S.) *grayi katokiyomasai* Shikama and Hasegawa from the sea-floor of Bisan-seto housed in Kagoshima University, C. (S.) *pulchellus* Imaizumi from Tsushima Island, C. (S.) *n. mageshimae* Kuroda et Okada from Tanegashima Island, C. (S.) *n. yakushimae* Kuroda et Okada from Yakushima Island after Matsumoto et al. (1984) and *Capreolus capreolus bedfordi* Thomas from the Korean peninsula housed in the National Science Museum, Tokyo (Reg. no. M 11126), and is almost the same size as *Cervus (C.) elaphus siciliae* Pohlig from Sicily, Italy after Gliozzi et al. (1993) (Figure 6). However, the skull is small in comparison to the Japanese megacerid *Sinomegaceros yabei* (Shikama) from the Seto Inland Sea off Matsuyama, Japan housed in Kagoshima University, *Elaphurus davidianus* Milne-Edwards housed in the National Science Museum, Tokyo (Reg. no. M 13066) and the European red deer such as C. (C.) *e. hippelaphus* Exleben and C. (C.) *e. acoronatus*

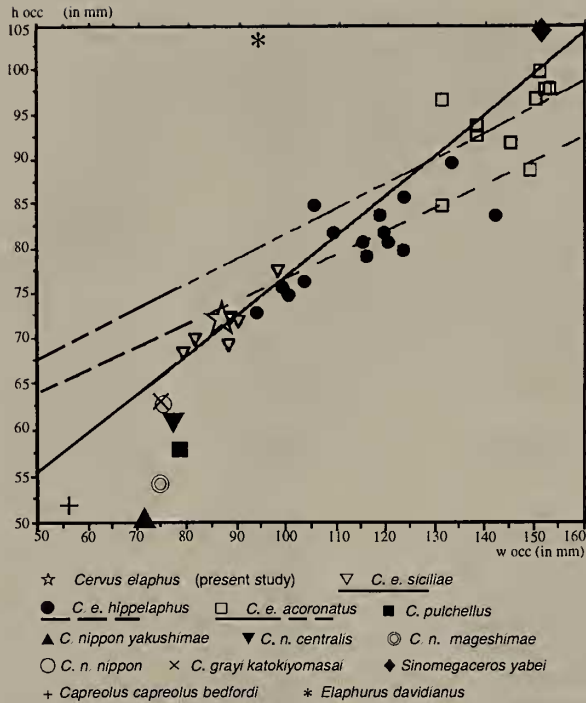


Figure 6. Scatter diagram and regression lines showing the relationship between (w_{occ}) and (h_{occ}) of the occipitals in *Cervus* (*Cervus*) *elaphus* studied in this paper, *C. (C.) e. siciliae*, *C. (C.) e. acoronatus*, *C. (C.) e. hippelaphus* (data after Gliozzi et al., 1993), *C. (Sika) pulchellus*, *C. (S.) nippon mageshimae*, *C. (S.) n. yakushimae* (data after Matsumoto et al., 1984), *C. (S.) n. nippon* from Kirishima, Japan, *C. (S.) grayi katokiyomasai* from the sea-floor of the Bisan-seto, Japan, *C. (S.) n. centralis* from Chichibu, Japan, *Sinomegaceros yabei* from the Seto Inland Sea, Japan housed in Kagoshima University, *Elaphurus davidianus* and *Capreolus capreolus bedfordi* from the Korean peninsula, Korea housed in the National Science Museum, Tokyo (Reg. no. M 13066 and M 11126, respectively).

Beninde after Gliozzi et al. (1993) based on the statistical data of Gliozzi et al. (1993) that summarize the relationships between occipital height and width (Figure 6).

The neurocranium proportion, with a width/height ratio of 1.14, seems close to those of *C. (C.) elaphus* subspecies such as *C. (C.) e. siciliae* (1.12–1.21), *C. (C.) e. acoronatus* (1.15) and *C. (C.) e. priscus* Kaup (1.12–1.20) from Mauer, Germany after Stefano and Petronio (1992). They are also comparable to *C. (S.) g. katokiyomasai* (1.06) and *C. (S.) nippon* subspecies such as *C. (S.) n. nippon* (1.23) and *C. (S.) n. centralis* (1.12), but they are quite different from other Cervinae species such as *E. davidianus* (0.97), *C. (Rusa) unicolor* Bechstein (0.97) housed in the National Science Museum, Tokyo (Reg. no. M 8932), *C. (A.) axis* (1.27), *C. (Nipponicervus) praenipponicus* Shikama (1.24–1.33) after Fossil Deer Research Group of Ichihara (1994) and *C. (Przewalskium) albirostris* Przewalski (1.45) after Flerov (1952). In lateral view, the angle between the parietal and frontal bones (113.6°) is almost identical to *C. (C.) elaphus* subspecies like *C. (C.) e. siciliae* ($111\text{--}123^\circ$), *C. (C.)*

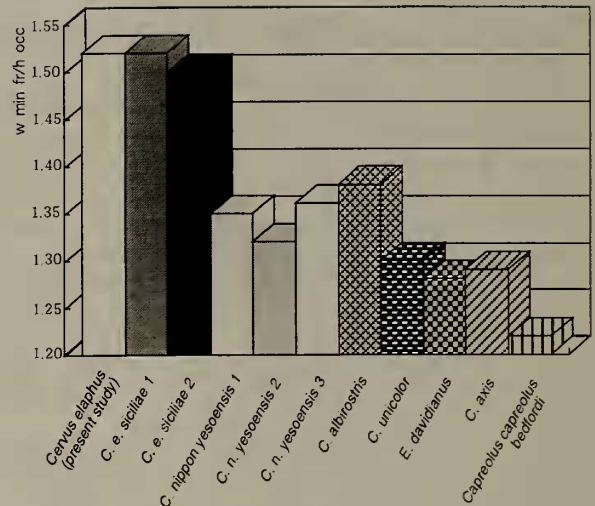


Figure 7. Bar graph showing the minimum frontal width/occipital height in *Cervus* (*Cervus*) *elaphus* (present study), *C. (C.) e. siciliae* (data after Gliozzi et al., 1993), *C. (Sika) nippon yesoensis* from Ashoro, Japan (data after Fossil Deer Research Group of Ichihara, 1994), *C. (Rusa) unicolor*, *Elaphurus davidianus*, *Capreolus capreolus bedfordi* from the Korean peninsula, Korea housed in the National Science Museum, Tokyo (Reg. nos. M 8932, M 13066 and M 11126, respectively), *Cervus* (*Przewalskium*) *albirostris* (data after Flerov, 1952) and *C. (Axis) axis* from India housed in the Nagoya Higashiyama Zoo, Japan. The ratio for fossil red deer (present study) is nearly identical with the values of *C. (C.) e. siciliae*.

e. priscus ($112\text{--}125^\circ$) and *C. (C.) e. acoronatus* (117°). It is also comparable to *C. (P.) albirostris* (107°), *C. (S.) g. katokiyomasai* (122°), *E. davidianus* (113°) and *C. (S.) nippon* subspecies such as *C. (S.) n. nippon* (110°) and *C. (S.) n. centralis* (128°), but it is definitely smaller than *C. (R.) unicolor* (142°), *Dama dama* Smith (136°) after Flerov (1952) and *C. (C.) e. canadensis* Erxleben (135°) from Canada housed in the National Science Museum (Reg. no. M 1094). The ratio of minimum width of frontal/occipital height (1.52) of the fossil skull is nearly identical to that of *C. (C.) e. siciliae* (1.50–1.52), but differs from those of *C. (P.) albirostris* (1.38), *C. (R.) unicolor* (1.30), *E. davidianus* (1.28), *C. (A.) axis* (1.29), *Capreolus capreolus bedfordi* (1.22) and *C. (S.) n. yesoensis* (Heude) (1.32–1.36) from Ashoro, Japan after Fossil Deer Research Group of Ichihara (1994) (Figure 7).

The protruding of the frontal suture is not so marked as in *C. (C.) e. canadensis*. In dorsal view the posterior margin of the roof does not curve posteriorly as much as that of *E. davidianus*. In the fossil, the ratio of maximum width between supraorbital foramina/occipital width is 0.76. This value is close to the known range (0.65–0.72) of several Cervinae species except for *C. (R.) unicolor* (0.49) and *C. (A.) axis* (0.47). UCKM-V-1 differs from skulls of large-sized Cervinae like *C. (C.) e. canadensis*, *E. davidianus* and *C. (R.) unicolor* in lacking additional nerve foramina above each supraorbital foramen. In posterior view the occipital is subcircular in shape like *C. (N.) praenipponicus* and subspecies of *C. (C.) elaphus* and *C. (S.) nippon* while that of *C.*

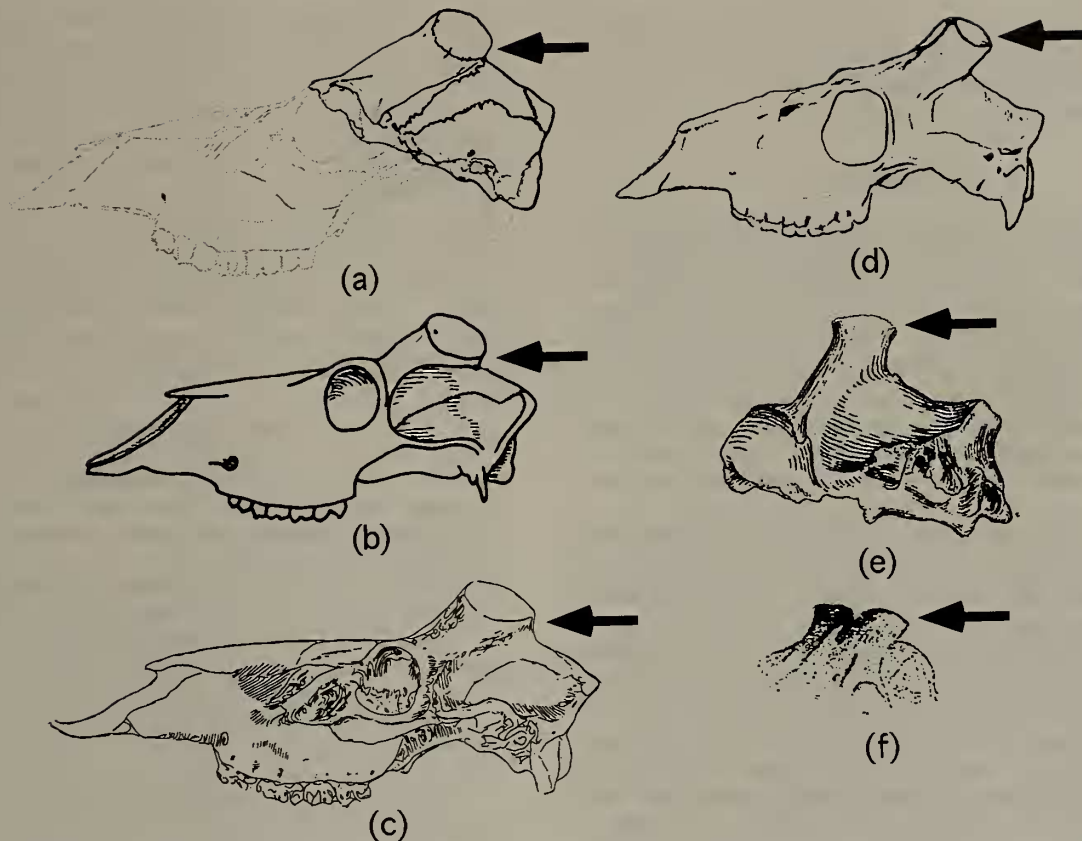


Figure 8. Diagram showing the different features of pedicles in the skulls of (a) *Cervus (Cervus) elaphus* studied in this paper, (b) *C. (C.) e. siciliae* (data after Gliozzi *et al.*, 1993), (c) *C. (C.) e. canadensis* (data after Flerov, 1952), (d) general *C. (Sika) nippon*, (e) *C. (S.) grayi* (data after Pei *et al.*, 1958) and (f) *C. (Rucervus) eldi* (data after Lydekker, 1898). Notice that *C. (S.) nippon*, *C. (S.) grayi* and *C. (R.) eldi* have pedicles that overhang the surface of the parietal.

(*S.*) *g. katokiyomasai* is trapezoidal in shape. In lateral view, the surface of the occipital is not so convex as in *D. dama*, *C. (S.) g. katokiyomasai* and *Capreolus capreolus bedfordi*. In ventral view the occipital condyles and the basioccipital are bounded by well-developed constriction unlike *Cervus (N.) praenipponicus*.

The angle of pedicle diversion (66°) is comparable to subspecies of *C. (C.) elaphus* like *C. (C.) e. siciliae* ($61-78^\circ$), *C. (C.) e. yarkandensis* Blanford (60°), *C. (C.) e. affinis* Hodgson ($62-70^\circ$) after Gliozzi *et al.* (1993) and *C. (C.) e. canadensis* (64°). It is also close to those of *C. (P.) albirostris* (68°), *C. (S.) g. katokiyomasai* (62°), *D. dama* (71°) and *C. (S.) nippon* subspecies such as *C. (S.) n. nippon* (63°) and *C. n. centralis* (73°). But it is greater than *C. unicolor* (48°) and *Capreolus capreolus bedfordi* (51°), and less than *E. davidianus* (78°). The ratio of minimum distance between pedicles/occipital width (0.88) is nearly identical to that of *Cervus (C.) elaphus siciliae* (0.89-0.90), but is different from other Cervidae species such as *C. (C.) e. canadensis* (0.61), *C. (P.) albirostris* (0.52), *C. (S.) g. katokiyomasai* (0.80), *C. (R.) unicolor* (0.73), *E. davidianus* (1.03) and *Capreolus capreolus bedfordi* (0.54). The pedicles are not flat transversely as seen in *Cervus (N.) praenipponicus*

collected from the Osaka Group. In lateral view the pedicles on the fossil skull are not inclined backwards as much as they are in *C. (S.) n. centralis*, *C. (N.) praenipponicus* and *C. (R.) unicolor*. In addition, they are considerably shorter and stouter like *C. (C.) e. siciliae* and *C. (C.) e. canadensis* after Flerov (1952), and do not overhang the parietal surface as seen in *C. (Rucervus) eldi* Beevan after Lydekker (1898), *C. (S.) grayi* Zdansky from Tingsun, China after Pei *et al.* (1958) and subspecies of *C. (S.) nippon* (Figure 8).

Based on these comparisons, we conclude that the fossil skull most closely resembles the red deer *Cervus (Cervus) elaphus* Linnaeus and therefore we assign it to that species.

Remarks.—The small size of the fossil specimen may justify recognition of a new subspecies endemic to Japan in the same way that the fossil deer *Cervus elaphus siciliae* Pohlig has been distinguished from Pleistocene deposits in the Mediterranean Sea (Gliozzi *et al.*, 1993). The proposal of a new subspecies is, however, postponed until additional well-preserved specimens are discovered. The fossil specimen has undergone some degree of alteration and is dark brown in color. The surface of the fossil is coated with well-rounded and well-sorted quartz grains of sand dune

origin. We can infer from its good state of preservation that this fossil was not transported by a river system from the Asian continent, but was probably buried near the site of the animal's death.

Discussion

Recent paleoceanographic researches suggested that Japan had lost its connection with Asia, except for the land bridge between Hokkaido and Sakhalin, in the last glacial period (Oba et al., 1984; Oba, 1984). From a paleobiogeographic point of view, it is also suggested that land mammals could not migrate from the Korean peninsula to Japan via the Tsushima Strait in the late Pleistocene, although they could have migrated to Honshu via Hokkaido from Sakhalin (Kamei, Kawamura and Taruno, 1988; Kamei, Taruno and Kawamura, 1988; Kawamura, 1982; Kawamura et al., 1989, etc.).

In order to estimate the geologic age of the fossil red deer, we have conducted ^{14}C dating, with a Tandetron accelerator mass spectrometer (AMS) at Nagoya University, on carbon from collagen fractions extracted from a part of fossil skull of *C. elaphus*. The ^{14}C age of $19,780 \pm 190$ yr BP was obtained for the fossil red deer from the sea-floor of the East China Sea. The geologic age of the fossil agrees with the accepted ^{14}C age (around 18,000 yr BP) of the Last Glacial maximum. The present finding of the fossil red deer strongly indicates that during the Last Glacial maximum the Asian continent and Kyushu were connected by a land bridge in the northern part of East China Sea.

The red deer *Cervus elaphus* first appeared in the early Middle Pleistocene of Europe (Kurtén, 1968). During the Middle to Late Pleistocene it dispersed throughout the mid-latitude zone of the Eurasian continent (Geist, 1971). The fossil occurrence of red deer from the East China Sea off Ushibuka City, western Kyushu, indicates the migration of this species to Japan at the Last Glacial period. During the Pleistocene, this widespread species evolved into a number of subspecies that today exhibit an adaptive response to regional environmental conditions on both the Eurasian and North American continents (Putman, 1988).

It has been shown that the living red deer *Cervus elaphus* and the sika deer *Cervus nippon* can hybridize in the natural state in the sympatric zones of the eastern Asian continent despite their differences in body size (Mirosl'ubov, 1949, etc.). A sika-like deer first appeared in the early Pleistocene of the Asian continent and seems to have been ancestral to *Cervus elaphus* (Geist, 1971). Though dispersal and speciation processes of these species remain unsolved, future molecular, morphologic and palaeontologic studies will clarify the phylogenetic relationship between the red deer and sika deer.

Acknowledgments

We are deeply indebted to Elsa Gliozzi and Carmelo Petronio of the Dipartimento di Scienze della Terra, Università degli Studi La Sapienza, Roma for their critical reading of an earlier draft of this paper and for their discussions and

suggestions concerning the taxonomy of the red deer. We are also indebted to Thomas A. Demere of the Department of Paleontology, San Diego Natural History Museum for reviewing the manuscript. We are grateful to Yoshikazu Hasegawa, Professor Emeritus of Yokohama National University, for allowing us to use his personal library and for fruitful discussions with us. Our sincere thanks are also extended to Tetsuro Tateshi who loaned us the fossil skull for this study and provided locality and collection data. We are also indebted to Hideki Endo of the National Science Museum, Tokyo, Tadashi Watanabe of Nagoya Higashiyama Zoo and Yasuhiro Sato of Kyushu African Safari Zoo who kindly allowed us to examine skulls of living deer.

References cited

- Boule, M., Breuil, H., Licent, E. and Teilhard de Chardin, P., 1928: Le Paléolithique de la Chine. *Archives de l'Institut de paléontologie humaine: Mémoire*, vol. 4, p. 1-138. (in French)
- Driesch, A., 1976: A guide to the measurement of animal bones from archaeological sites. *Peabody Museum of Harvard University, Massachusetts*, p. 27-57.
- Flerov, C.C., 1952: Musk deer and deer, *Fauna of U.S.S.R.*, vol. 1, no. 2, 257 p. Academic Science of U.S.S.R. (English translation U.S. Dept of Commerce), Washington, D.C.
- Fossil Deer Research Group of Ichihara, 1994: Morphological study on *Cervus (Nipponicervus) praenipponicus* Shikama from the Upper Pleistocene in the northern part of Boso Peninsula. *Earth Science*, vol. 48, no. 3, p. 181-207. (in Japanese)
- Geist, V., 1971: The relation of social evolution and dispersal in ungulates during the Pleistocene, with emphasis on the Old World deer and the genus *Bison*. *Quaternary Research*, vol. 1, p. 283-315.
- Gliozzi, E., Malatesta, A. and Scalone, E., 1993: Revision of *Cervus elaphus siciliae* Pohlig, 1893, late Pleistocene endemic deer of the Siculo-Maltese District. *Geologica Romana*, vol. 29, p. 307-353.
- Kamei, T., Kawamura, Y. and Taruno, H., 1988: Mammalian stratigraphy of the late Neogene and Quaternary in the Japanese Island. *Memoirs of the Geological Society of Japan*, vol. 30, p. 181-204. (in Japanese)
- Kamei, T., Taruno, H. and Kawamura, Y., 1988: Implication of mammal fauna for the Quaternary geohistory of the Japanese Islands. *Quaternary Research*, vol. 26, p. 293-303. (in Japanese)
- Kawamura, Y., 1982: Biogeographical aspects of the Quaternary mammals of Japan. *Mammalian Science*, vol. 43/44, p. 99-130. (in Japanese)
- Kawamura, Y., Kamei, T. and Taruno, H., 1989: Middle and late Pleistocene mammalian faunas in Japan. *Quaternary Research*, vol. 28, p. 317-326. (in Japanese)
- Kurtén, B., 1968: *Pleistocene Mammals of Europe*, 317 p. Weidenfeld and Nicolson, London.
- Lowe, V.P.W. and Gardiner, A.S., 1989: Are the new and old world wapitis (*Cervus canadensis*) cospecific with red deer (*Cervus elaphus*)? *Journal of Zoology, Society of London*, vol. 218, p. 51-58.
- Lydekker, R., 1898: *The deer of all lands*, 329 p. Rowland Ward, London.

- Matsumoto, H., 1926: On some fossil cervids from Shantung, China. *Science Reports of the Tohoku University, 2nd Series*, vol. 10, no. 2, p. 27-37, pls. 12-15.
- Matsumoto, M., Nishinakagawa, H. and Otsuka, J., 1984: Morphometrical study on the skull of *Cervus pulchellus*, *Cervus nippon mageshimae* and *Cervus nippon yakushimae*. *Journal of the Mammalogical Society of Japan*, vol. 10, no. 1, p. 41-53. (In Japanese)
- Mirol'ubov, I.I., 1949: Gibridizacija pjatnistogo olenja s izjubrom [The hybridization between sika and iz'ubra red deer]. *Karakulevodstvo i zverovodstvo*, p. 74-75. (in Russian)
- Oba, T., 1984: The oxygen and carbon isotopes. *Earth Monthly*, vol. 6, p. 558-566. (in Japanese)
- Oba, T., Omura, A., Kato, M., Kitazato, H., Koizumi, I., Sakai, T., Takayama, T. and Mizota, T., 1984: The palaeoenvironmental change. *Earth Monthly*, vol. 6, p. 571-575. (in Japanese)
- Otsuka, H., 1982: The Cenozoic vertebrate fauna of Kyushu and the Ryukyu Islands, West Japan, viewed from the faunal relation to those of the Asiatic Continent. *Proceeding of Memorial Symposium on the 100th Meeting of the Nishinihon Branch, Geological Society of Japan*, p. 109-116. (in Japanese)
- Otsuka, H., 1987: Middle- and Late Pleistocene mammalian faunae in the Japanese Islands with special reference to the mammalian fauna of the Nishiyagi Formation in Akashi District. *Bulletin of the National Museum of Japanese History*, vol. 13, sec. 6, p. 275-287. (in Japanese with English abstract)
- Pei, W.C., 1940: The upper cave fauna of Choukoutien. *Palaeontologia Sinica, New Series C*, vol. 10, p. 1-84.
- Pei, W.C., Woo, J.K., Chia, L.P., Chou, M.Z., Liu, H.T. and Wang, C.Y., 1958: Report on excavation of Palaeolithic sites at Tingtsun, Hsiangtensien, Shansi Province, China. *Institute of Vertebrate Palaeontology, Academy of Sinica, Series 1, Monograph*, no. 2, p. 1-111, 46 pls. (in Chinese)
- Putman, R., 1988: *The natural history of deer*, 191 p. Christopher Helm, London.
- Shikama, T., 1941: Fossil deer in Japan. *Jubilee Publication in the Commemoration of Professor H. Yabe's 60th Birthday*, vol. 2, p. 1125-1170.
- Shikama, T., 1949: The Kuzuü Ossuaries. Geological and palaeontological studies of the limestone fissure deposits in Kuzuü, Totigi Prefecture. *Science Reports of the Tohoku University, 2nd Series*, vol. 23, p. 1-209.
- Stefano, G.D. and Petronio, C., 1992: New data on *Cervus elaphus acoronatus* Beninde on the European Pleistocene. *Bollettino della Societa Paleontologica Italiana*, vol. 31, no. 3, p. 295-315. (in Italian)
- Tokunaga, S. and Naora, N., 1934: Report of diggings at Ho-Chia-Kou, Ku-Hsiang-Tung, Kirin, Manchoukuo. *Report of the First Scientific Expedition to Manchoukuo*, sec. 2, pt. 1, p. 1-119. (in Japanese)
- Tokunaga, S. and Naora, N., 1939: Fossil remains excavated at Ku-Hsiang-Tung near Harbin, Manchoukuo. *Report of the First Scientific Expedition to Manchoukuo*, sec. 2, pt. 4, p. 1-229. (in Japanese)
- Vangengeim, E.A. and Sher, A.V., 1971: Siberian equivalents of the Tiraspol faunal complex. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 8, p. 197-207.
- Whitehead, G.K., 1972: *Deer of the world*, 194 p. Constable, London.